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Acido- and neutrophilic temperate forest plants display distinct shifts in ecological pH niche across north-western Europe

J. Reinecke, M. Wulf, L. Baeten, J. Brunet, G. Decocq, P. De Frenne, M. Diekmann, B. J. Graae, T. Heinken, M. Hermy, A. Jamoneau, J. Lenoir, J. Plue, A. Orczewska, H. Van Calster, K. Verheyen and T. Naaf

J. Reinecke (*jennifer.reinecke@senckenberg.de*), Dept of Botany, Section Phanerogams I, Senckenberg Natural History Museum Görlitz, Görlitz, Germany. – M. Wulf and T. Naaf, Inst. of Land Use Systems, Leibniz-Centre for Agricultural Landscape Research (ZALF) Müncheberg, Germany. – L. Baeten, P. De Frenne and K. Verheyen, Forest and Nature Lab, Ghent Univ., Gontrode-Melle, Belgium. – J. Brunet, Southern Swedish Forest Research Centre, Swedish Univ. of Agricultural Sciences, Alnarp, Sweden. – G. Decocq, A. Jamoneau and J. Lenoir, UR «Ecologie et Dynamique des Systèmes Anthropisés» (EDYSAN, FRE 3498 CNRS-UPJV), Amiens, France. – M. Diekmann, Vegetation Ecology and Conservation Biology, Inst. of Ecology, FB2, Univ. of Bremen, Bremen, Germany. – B. J. Graae, Dept of Biology, Norwegian Univ. of Science and Technology, Trondheim, Norway. – T. Heinken, Biodiversity and Systematic Botany, Inst. of Biochemistry and Biology, Univ. of Potsdam, Potsdam, Germany. – M. Hermy, Division Forest, Nature and Landscape, Univ. of Leuven, Leuven, Belgium. – J. Plue, Dept of Physical Geography and Quaternary Geology, Stockholm Univ., Stockholm, Sweden. – A. Orczewska, Dept of Ecology, Univ. of Silesia, Katowice, Poland. – H. Van Calster, Research Inst. for Nature and Forest (INBO), Brussels, Belgium.

Ecological niches of organisms vary across geographical space, but niche shift patterns between regions and the underlying mechanisms remain largely unexplored. We studied shifts in the pH niche of 42 temperate forest plant species across a latitudinal gradient from northern France to boreo-nemoral Sweden. We asked 1) whether species restrict their niches with increasing latitude as they reach their northern range margin (environmental constraints); 2) whether species expand their niches with increasing latitude as regional plant species richness decreases (competitive release); and 3) whether species shift their niche position toward more acidic sites with increasing latitude as the relative proportion of acidic soils increases (local adaptation). Based on 1458 vegetation plots and corresponding soil pH values, we modelled species response curves using Huisman–Olf–Fresco models. Four niche measures (width, position, left and right border) were compared among regions by randomization tests. We found that with increasing latitude, neutrophilic species tended to retreat from acidic sites, indicating that these species retreat to more favorable sites when approaching their range margin. Alternatively, these species might benefit from enhanced nitrogen deposition on formerly nutrient-poor, acidic sites in southern regions or lag behind in post-glacial recolonization of potential habitats in northern regions. Most acidophilic species extended their niche toward more base-rich sites with increasing latitude, indicating competitive release from neutrophilic species. Alternatively, acidophilic species might benefit from optimal climatic conditions in the north where some have their core distribution area. Shifts in the niche position suggested that local adaptation is of minor importance. We conclude that shifts in the pH niche of temperate forest plants are the rule, but the directions of the niche shifts and possible explanations vary. Our study demonstrates that differentiating between acidophilic and neutrophilic species is crucial to identify general patterns and underlying mechanisms.

There is a long-standing awareness among ecologists that the ecological response of organisms to environmental factors varies across geographical space (Turesson 1922, Walter and Walter 1953, Passarge 1958, van Valen 1965). Turesson (1922) noted the importance of considering varying ecological responses of different populations of the same species in synecological studies. For instance, bird species have wider feeding niches on islands than on the mainland (van Valen 1965), and forest plant species change their phytosociological behavior along a longitudinal gradient from western to eastern parts of the central European lowlands (Passarge 1958). A species' response toward environmental conditions is a result of both its physiology (fundamental niche) and

biotic interactions in natural communities (realized niche, Hutchinson 1957). We here define a niche shift as the sum of changes in the niche position (environmental conditions at maximum probability of occurrence) and the niche width (environmental range where the species occurs) of a species between two or more regions (cf. Wasof et al. 2013). Using field observations, it is possible to analyze only shifts in the realized niche; thus, unless otherwise indicated, the following is concerned with the realized niche.

Understanding the patterns of niche shifts and their underlying mechanisms is essential to make reliable predictions of species' responses to environmental change (Morin and Thuiller 2009). Species distribution models

(SDMs), for example, are used to predict species' responses to environmental changes, such as soil acidification or global warming (Randin et al. 2006, Pearman et al. 2008, Morin and Thuiller 2009). However, today's niche-based models are usually not easily transferable to other regions as they fail to incorporate niche differences between regions (Randin et al. 2006, Hájková et al. 2008). Predictions of species' responses to environmental change and subsequent conservation strategies will remain uncertain as long as niche shift patterns are not understood and incorporated.

In plant ecology, changes in species' responses to soil pH have received particular attention because pH is an easily-measured chemical soil variable, widely used as a proxy for soil fertility, i.e. an environmental factor acting directly on plant growth (Austin 1980), and is a major determinant of species occurrence in many plant communities (Ellenberg 1988). Many studies have addressed niche shifts in the context of plant response to soil pH (Diekmann and Lawesson 1999, Prinzing et al. 2002, Coudun and Gégout 2005, Hájková et al. 2008, Wasof et al. 2013). However, the reported niche shift patterns and the assumed underlying mechanisms differ considerably. Some early observations indicate that some species restrict their niches from the center of their range toward the margins (Passarge 1958). These observations include both acidophilic species restricting their niches toward more acidic sites (Hájková et al. 2008) and neutrophilic species restricting their niches toward more base-rich sites at their range margin (Diekmann and Lawesson 1999). It has been proposed that species compensate the deterioration of overall living conditions at the range margin, e.g. in terms of macroclimate, by retreating to the sites with the most favorable environmental conditions, e.g. in terms of microclimate, soil conditions or the availability of mutualistic species, like mycorrhizal fungi (Brown 1984, Brussard 1984, Walter and Breckle 1991, Leuschner et al. 2009). A contraction of the realized niche at a species' range margins can also be a consequence of lower genetic variation within range-margin populations (Brussard 1984, Mandák et al. 2005). Despite these possible mechanisms to explain narrower niches at species' range margins, several studies found no support for the range-margin hypothesis (Diekmann and Lawesson 1999, Prinzing et al. 2002, Hájková et al. 2008, Leuschner et al. 2009). Instead, some studies have found no systematic niche shifts from the core of species' ranges toward their range margins (Prinzing et al. 2002, Leuschner et al. 2009) or even found broader niches toward species' range margins (Diekmann and Lawesson 1999, Hájková et al. 2008). Niche extensions are better explained by competitive release in some of these studies. This hypothesis states that a species may occupy a wider part of its fundamental niche when competition decreases (MacArthur 1972). Indeed, a positive relationship between extensions of the niche and reduced competition from north-eastern toward north-western France has been found (Coudun and Gégout 2005). Hájková et al. (2008), however, found that the niche width of most species increased toward acidic sites between regions despite a growing pool of acidophilic species.

Both the range margin and competitive release hypotheses refer to changes in niche width. Concerning shifts in the niche position, Wasof et al. (2013) observed that as the relative frequency of base-rich soils decreased toward the north, the

niche position shifted toward more acidic sites. According to the local adaptation hypothesis, the niche position follows the general trend of shifts in environmental conditions as local populations are better adapted to their home environments than foreign populations (Leimu and Fischer 2008). On the one hand, adaptation to local environmental conditions may result in genetically different ecotypes within a species (Turesson 1922, Hájková et al. 2008) and thus in different fundamental and subsequently realized niches of the populations. On the other hand, species may adapt to local conditions by adjusting their phenotypes (Valladares et al. 2014).

Obviously, the observed patterns of niche shifts and the assumed underlying mechanisms differ among studies. Two likely reasons for these inconsistencies are differences in the geographical gradients studied and the methods used to quantify species' niche shifts. Most studies compare only two regions across short distances (but see Diekmann and Lawesson 1999, Wasof et al. 2013). The size of the geographical extent of the study area has been identified to be a key factor for being able to detect niche shifts (Wasof et al. 2013), so further analyses across the European continent using large numbers of sample sites have been recommended (Gégout and Krizova 2003, Coudun and Gégout 2005). The quantification of species' niches has often been based on co-occurrence data, such as phytosociological units, ordination scores and mean indicator values. Co-occurrence-based metrics are strongly dependent on species composition and thus are useful for detecting shifts in the multidimensional realized niche (Wasof et al. 2013). Response-curve modeling on the basis of actually measured environmental conditions (here pH measurements) is a valuable complementary approach in regard to single niche dimensions. This approach is less often applied (but see Coudun and Gégout 2005, Hájková et al. 2008) because data on species occurrence along with environmental measurements is more difficult to obtain in large numbers and across large geographical extents. Applying response curve modeling also allows determination of the direction of niche shifts regarding niche borders, which makes an interpretation of niche shifts more precise.

Here, we studied the niche shifts of 42 herbaceous, vascular temperate forest plant species across a large latitudinal gradient from northern France to boreo-nemoral Sweden. This spatial gradient also represents a gradient of habitat conditions for temperate forest plants because a) many deciduous forest plants approach their distributional range margin at the northern margin of the nemoral or boreo-nemoral zones (Hultén and Fries 1986); b) regional vascular plant diversity decreases toward the north (Barthlott et al. 2007), and therefore competitive restriction of niches may be reduced (MacArthur 1972); and c) the relative frequency of acidic soils generally increases toward the north (Reuter et al. 2008, Wasof et al. 2013). As earlier observations suggest a differentiation between acidophilic and neutro-/basophilic species, we hypothesize the following opposing (but not necessarily mutually exclusive) niche shift patterns (Table 1). Note that we aim at testing general patterns of niche shifts, while discussing, but not testing the mechanisms behind these patterns, as this is not possible using our approach. For better readability and understanding we will, nonetheless, name our hypothesis according to the mechanisms from which they were derived.

Table 1. Hypothesized latitudinal trends (increasing (/) or decreasing (\) toward the north) in niche measures (WID – niche width, LB – left border, RB – right border, POS – niche position) according to three mechanisms that lead to niche shifts across space 1) range margin, 2) competitive release and 3) local adaptation.

No.	Possible mechanism	Species group	Expected trends in niche measures with increasing latitude			
			WID	LB	RB	POS
H1	Approaching the range margin		\			
	a) acidophilic	acidophilic	\		\	
	b) neutrophilic	neutrophilic	\	/		
H2	Competitive release		/			
	a) acidophilic	acidophilic	/		/	
	b) neutrophilic	neutrophilic	/	\		
H3	Local adaptation					\

H1 (range-margin hypothesis): with increasing latitude, forest plant species restrict their niche as they reach their northern range margin, with a) acidophilic species restricting their niche to acidic sites and b) neutrophilic species restricting their niche to the most base-rich sites.

H2 (competitive-release hypothesis): with increasing latitude, forest plant species expand their niches as regional plant species richness decreases, with a) acidophilic species expanding their niche toward more base-rich sites and b) neutrophilic species expanding their niche toward more acidic sites.

H3 (local-adaptation hypothesis): with increasing latitude, forest plant species shift their pH niche position

toward more acidic sites as the relative proportion of acidic soils increases.

Material and methods

Data collection

We collected data from four regions in temperate Europe along a latitudinal gradient from Belgium/northern France over northern Germany and Denmark/Scania to boreo-nemoral Sweden (Fig. 1). All datasets comprised vegetation relevés in temperate broadleaved forests with associated soil

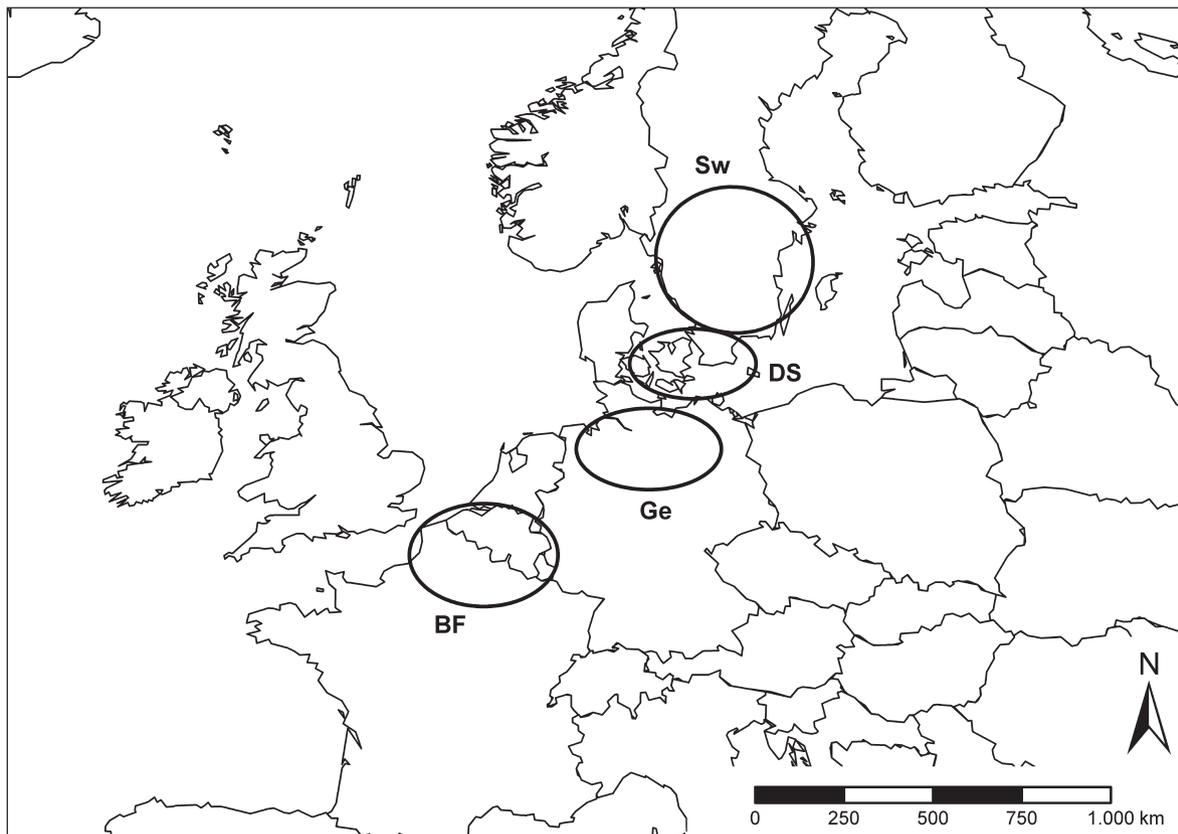


Figure 1. Study regions along the latitudinal gradient from Belgium/France (BF) over Germany (Ge) and Denmark/Scania (DS) to boreo-nemoral Sweden (Sw).

pH measurements for each plot. From the original datasets, we selected plots with the aim to keep other determinants of plant species occurrence as constant as possible. The following criteria were applied: 1) all plots had to be located in stands with a long forest continuity (> ca 200 yr) and undisturbed herbaceous layer so that a strong species–environment relationship could be assumed. 2) The tree layer had to be dominated by broad-leaved tree species, i.e. the cover of coniferous tree species should not exceed 20%. 3) The stands had to be mature or at least beyond the pole wood stage and should not show signs of recent (management) disturbance, i.e. no large canopy gaps and no driving tracks or other soil damage should be present. 4) Soil moisture, measured by unweighted mean Ellenberg indicator value (Ellenberg et al. 2001), had to be in the range $4.5 \leq F \leq 6$ to exclude very dry and wet sites and thus avoid confounding the effects of soil moisture on soil pH. 5) All plots had to be located in the lowland (< 300 m a.s.l.) to avoid any confounding effects of altitude on the effects of latitude.

The final dataset comprised 1458 vegetation plots, 322 plots from Belgium/France, 480 plots from Germany, 452 plots from Denmark/Scania and 204 plots from boreo-nemoral Sweden (Table 2). The soil pH in most plots (1415 plots) had been measured in KCl, based on soil samples taken from the upper 10 cm of mineral soil (i.e. after litter layer removal). The remaining pH values were converted to this standard by applying regression models (Supplementary material Appendix 1). The pH gradient covered by the regional datasets differed slightly. We, therefore, restricted our analyses to plots within the pH range of 2.8 to 6.0, common to all four studied regions. This is the only way to make niche measures of truncated response curves comparable among regions. The pH gradient still spans multiple soil pH buffer ranges, from the aluminum over the cation exchange to the carbonate buffer range (Ulrich 1991). The nomenclature of species follows Jansen and Dengler (2008).

Niche modeling

Species selection

Reliable response curve modeling requires a certain minimum number of presences and absences (Jansen and Oksanen 2013); however, setting these values too high would have resulted in a small number of species for which response curves could be compared across all regions, reducing the generality of our study. As a trade-off, we subjectively decided that species had to be present in at least three of the

four regions with a minimum number of 20 presences and 20 absences in each region. This yielded 42 herb species for the subsequent analyses. Species with less than 20 absences in a region were treated as ‘indifferent’ per definition.

Response curve modeling

For each of the selected species, we calculated a separate response curve per region, using Huisman–Olf–Fresco (HOF) models (Huisman et al. 1993) and the R package ‘eHOF’ (Jansen and Oksanen 2013). HOF modeling is an extension of logistic regression that allows modeling a set of five response shapes, namely flat, monotonic, plateau-like, symmetric bell-shaped and skewed bell-shaped. We excluded 2 bimodal response shapes, because of the short pH gradient covered. This modeling technique provides a good compromise between model fit and complexity (Oksanen and Minchin 2002).

The number of plots included in the model may influence the shape of the response curve and the resulting niche measures. In addition, a species’ frequency may differ between regions due to variation in the pH niche and due to different survey designs that might be biased toward the collection of certain species, habitats or other biogeographical factors (Manthey et al. 2011, Wasof et al. 2013). We, therefore, kept both sample size and frequency for each species constant across regions. For each species, we determined the largest possible sample size and the corresponding frequency as the sum of the minimum number of presences and absences across regions. Subsampling was carried out at random without replacement (see below).

The uncertainty of a HOF-model increases if sampling is uneven across the gradient (Peppeler-Lisbach 2008, Jansen and Oksanen 2013), so we corrected for a non-uniform coverage of the pH gradient. First, we divided the pH gradient into 13 intervals with a width of 0.25 pH units. Second, the inverse relative frequency of presences (absences) in each interval was used as the probability weight during the random subsampling for plots containing (not containing) the focal species (Peppeler-Lisbach 2008). Third, a total of 50 random subsets were used to create a stable average response curve from the fitted values of each subset. Finally, we created average curves by approximating the curves as a sequence of points with an increment of 0.01 pH units and averaging the corresponding points across regions.

We derived four measures from the averaged response curves to characterize a species’ pH niche: niche position (pH value at maximum probability of occurrence), left and right border (pH value where the curve falls below 25% of

Table 2. Characteristics of the herb species datasets from all four study regions.

Region	# plots	Mean weighted sampling year	Plot size (m ²)	# species	Data sources
Boreo-nemoral Sweden (Sw)	204	1989	100–400	214	Diekmann (1994)
Denmark/Scania (DS)	452	1984	400–900	309	Brunet (1993), Falkengren-Grerup and Tyler (1993), Brunet et al. (1996), Graae and Sunde (2000), Graae et al. (2004), Lenoir et al. (2013)
Northern Germany (Ge)	480	1998	100–900	228	Heinken (1995), Naaf and Wulf (2011), Plue et al. (2013), unpubl.
Belgium/northern France (BF)	322	2005	100–225	168	Lameire et al. (2000), Fastenaekels et al. (2003), Van Calster et al. (2007, 2008), Baeten et al. (2009, 2010), Jamoneau (2010)

a species' maximum probability of occurrence left and right of its niche position, respectively, (Heegard 2002, Štechová et al. 2008)) and niche width (pH range between the left and right border). For plateau-like response curves, the niche position was estimated as the mean of the plateau. If the true niche position lies beyond the part of the pH gradient we studied, the calculated niche position is equal to either one of the niche borders.

Between-region comparison of niches

We compared the niche measures for each species between regions in a pair-wise permutation test. Thus, for a given niche parameter, we performed a maximum of six comparisons between all four regions, making a maximum of 24 comparison tests in total (Supplementary material Appendix 2). The rationale behind each test was that under the null hypothesis of equal niche measures in both regions, the plots could be randomly assigned to either of the regions. We repeated this permutation 499 times, each time using the same 50 subsets of plots as above. For each permutation, we calculated the average response curves across the 50 subsets, the niche measures and the difference in niche measures between the two regions. These differences were compared with the empirical differences of niche measures between regions. An observed difference was considered significant if less than 5% of all permutations resulted in the same or a larger absolute difference. The p-values were not adjusted for multiple testing to avoid committing a type II error (Moran 2003). The high number of significant differences in niche measures between regions that we found for most species indicates that these differences are unlikely to be chance effects (Supplementary material Appendix 2). Furthermore, we interpreted only differences beyond an empirically determined threshold of 0.4 pH units to ensure that the observed changes in niche measures across regions were due to real changes in the species' ecological behavior. Smaller thresholds yielded very individual and non-monotonous niche shift patterns that could not be generalized across species. Some response curves exhibited plateau-like optima. In these cases, differences in niche position between regions were only considered significant if neither niche position lay within the plateau of the other region. After visual inspection of the response curves, we defined plateaus as the range of pH values, in which the probability of occurrence did not differ more than 0.004 probability units from the maximum probability of occurrence across a minimum length of 0.8 pH units. We then searched for patterns in the changes of niche measures along the latitudinal gradient and generalized these into six types: monotonic increase/decrease with latitude, maximum/minimum at mid-latitude (i.e. in Germany and/or Denmark/Scania), no shift with latitude (invariant) and inconsistent differences among regions.

Hypothesis testing

We tested those hypotheses that do not differentiate between acidophilic and neutrophilic species by binomial exact tests. To test whether the niche width is more likely to decrease or

increase with latitude (H1 vs H2), we used a two-sided test. To test whether decreases in the niche position with latitude are more likely than increases (H3), we used a one-sided test.

Those hypotheses referring to either acidophilic (H1a and H2a) or neutrophilic species (H1b and H2b) were tested with two tests each, one for the niche width and one for the corresponding border (Table 1). For this purpose, we classified the species into acidophilic (mean niche position across regions $\text{pH} < 4.0$), neutrophilic (mean niche position across regions $\text{pH} > 5.0$) and intermediate species. Categorizing species as acidophilic from ecological optima is critical, and we are aware that some species labeled 'acidophilic' might actually be only acid tolerant. However, we retain the term 'acidophilic' to accentuate the contrast with neutrophilic species (cf. Coudun and Gégout 2005, Hájková et al. 2008) and will discuss any consequences of this simplification later.

For each test, we compiled a 2×2 contingency table with the rows distinguishing between species that show a monotonic increase/decrease with latitude in the tested niche measure and all other species, and with the columns distinguishing between acidophilic/neutrophilic species and all other species. Then, we applied Boschloo's unconditional exact tests (Lydersen et al. 2009) using the R package Exact (Calhoun and Calhoun 2013) to test for a significant association in each table. The tests were one-sided corresponding to the tested hypotheses. The p-values were not adjusted for multiple testing to avoid committing a type II error (Moran 2003).

Results

Universality of niche shifts along the latitudinal gradient

All 42 species responded to pH and occupied well-defined, realized pH niches in most of the regions (Table 3, Supplementary material Appendix 3). We found significant shifts across regions in at least one niche measure for all species: 36 species displayed a significant change in niche width, either concerning the left border, right border or both (Table 3). Most of the six species without significant change in niche width occurred along the entire pH gradient studied in all regions, so we cannot rule out any niche shifts beyond our restricted pH gradient. Thirty-six species displayed a shift in niche position. All of the six species without significant shifts had their niche position at or close to a truncated end of their response curve in each region; thus, again, we cannot rule out shifts in the niche position beyond our studied pH gradient. The shifts in the niche position seem to be unrelated to changes in the niche width (Table 3).

Niche shift patterns in relation to the hypotheses

Niche contraction vs niche expansion with increasing latitude (H1 vs H2)

Fourteen species (33.3%) displayed niche contractions with increasing latitude, and twelve species (28.6%) displayed niche expansions with increasing latitude (Fig. 2, Table 3).

Table 3. Latitudinal trends (increasing (/) or decreasing (\)) toward the north; largest (n) or smallest (u) at mid-latitudes; increasing toward Germany, decreasing toward Denmark/Scania, increasing toward the north again (nu); not shifting across regions (-) in niche measures (WID – niche width, LB – left border, RB – right border, POS – niche position) of all 42 species (a – acidophilic (< pH 4.0), n – neutrophilic (> pH 5.0); based on mean niche position across regions). The observed patterns of trends either support (H+) or do not support (H-) the hypotheses as mentioned in Table 1. Additional species attributes are given for the Ellenberg values for soil reaction (R) and nitrogen (N). Species with their main distribution in the boreal zone according to Oberdorfer (2001) are marked with 'n' (Nordic).

Species	R ¹	N ¹	Nordic	H+	H-	Trends in niche measures with increasing latitude			
						WID	LB	RB	POS
Narrower niche toward the north									
a <i>Agrostis capillaris</i>	4	4	n	1a	3	\	-	\	/
a <i>Dryopteris dilatata</i>	x	7	n	1a, 3		\	-	\	\
a <i>Dryopteris filix-mas</i>	5	6			1a, 3	\	/	-	/
n <i>Paris quadrifolia</i>	7	7		1b		\	/	-	\
n <i>Stachys sylvatica</i>	7	7		1b		\	/	-	u
n <i>Filipendula ulmaria</i>	x	4	n	1b		\	/	-	-
n <i>Geum urbanum</i>	x	7		1b		\	/	-	\
n <i>Aegopodium podagraria</i>	7	8		1b	3	\	/	-	/
<i>Anemone nemorosa</i>	x	x				\	/	-	n
<i>Athyrium filix-femina</i>	x	6	n			\	-	n	n
<i>Mercurialis perennis</i>	8	7		3		\	/	-	\
<i>Dactylis glomerata</i>	x	6		3		\	/	\	\
<i>Melica uniflora</i>	6	6		3		\	/	\	\
<i>Lonicera periclymenum</i>	3	4		3		\	-	\	\
Broader niche toward the north									
a <i>Deschampsia flexuosa</i>	2	3	n	2a		/	-	/	-
a <i>Melampyrum pratense</i>	3	2	n	2a		/	-	/	-
a <i>Pteridium aquilinum</i>	3	3	n	2a		/	-	/	-
a <i>Vaccinium myrtillus</i>	2	3	n	2a		/	-	/	-
a <i>Holcus mollis</i>	2	3		2a	3	/	-	/	/
a <i>Poa nemoralis</i>	5	4	n	2a	3	/	-	/	/
n <i>Galium aparine</i>	6	8		2b		/	\	-	u
n <i>Mycelis muralis</i>	x	6			2b, 3	/	/	/	/
<i>Moehringia trinervia</i>	6	7				/	\	/	\
<i>Oxalis acetosella</i>	4	6	n			/	n	/	n
<i>Ranunculus ficaria</i>	7	7				/	-	nu	n
<i>Ranunculus auricomus</i> agg.	7	x		3		/	\	-	\
Narrowest niche in central regions									
n <i>Polygonatum multiflorum</i>	6	5			3	u	n	-	/
n <i>Carex sylvatica</i>	6	5		3		u	n	-	-
<i>Circaea lutetiana</i>	7	7				u	n	-	n
Broadest niche in central regions									
a <i>Luzula pilosa</i>	5	4	n			n	-	n	-
a <i>Convallaria majalis</i>	x	4				n	-	n	u
n <i>Galium odoratum</i>	6	5				n	u	-	\
n <i>Urtica dioica</i>	7	8	n			n	/	/	/
<i>Stellaria holostea</i>	6	5				n	n	n	n
<i>Deschampsia cespitosa</i>	x	3	n		3	n	nu	/	/
<i>Milium effusum</i>	5	5				n	nu	-	nu
Invariant									
n <i>Geranium robertianum</i>	x	7		3		-	-	-	\
n <i>Lamium galeobdolon</i>	7	5				-	-	-	\
n <i>Viola reichenbachiana</i>	7	6		3		-	\	\	\
a <i>Dryopteris carthusiana</i>	4	3		3		-	-	-	\
<i>Galeopsis tetrahit</i>	x	6	n	3		-	-	-	\
<i>Maianthemum bifolium</i>	3	3	n	3		-	-	-	\

¹Ellenberg values range between 1 (indicating very acid soil conditions and very low nitrogen availability) and 9 (indicating very basic soil conditions and very high nitrogen availability). Species to which Ellenberg did not assign an indicator value are marked with an x.

The probabilities of niche width decreases or increases were not significantly different ($p = 0.845$). Ten species (23.8%) had their narrowest or broadest niche in central regions (Germany or Denmark/Scania). Six species (14.3%) showed an invariant niche width across regions.

Among those species contracting their niche toward the north, ten species (71.4%), retreated from acidic sites and

five species (35.7%) retreated from base-rich sites (Table 3). The niche width of neither acidophilic species (H1a) nor neutrophilic species (H1b) decreased more often than expected by chance (Fig. 2, Table 4). The number of acidophilic species that retreated from base-rich sites (H1a) was not unexpectedly large. However, neutrophilic species that retreated from acidic sites (H1b) occurred significantly

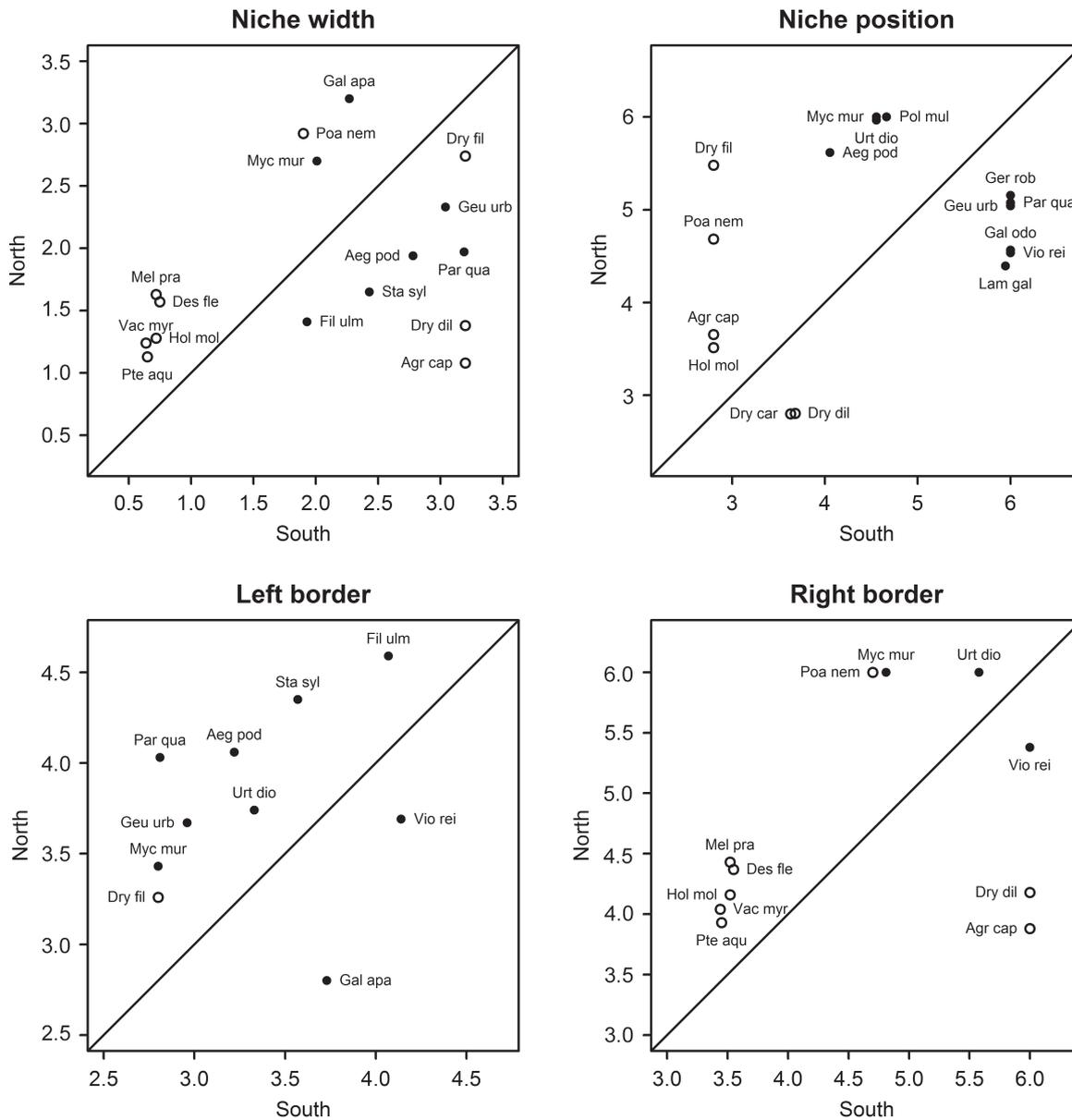


Figure 2. Differences in pH niche measures between southern (Belgium/France or Germany) and northern (Denmark/Scania or boreonemoral Sweden) latitudes for acidophilic (white dots) and neutrophilic (black dots) species with a monotonous trend of the corresponding niche measure along the latitudinal gradient. Abbreviations of species names consist of the first three letters of both the generic and specific epithet (full species names are given in Table 3).

more often than expected (Table 4, e.g. *Stachys sylvatica*, Fig. 3).

Among those species expanding their niche toward the north, nine species (75%) expanded their niche to more base-rich sites and only three species (25%) expanded their niche to more acidic sites. The acidophilic species displayed an increasing niche width and an increasing right border (H2a) significantly more often than expected by chance (Table 4, e.g. *Deschampsia flexuosa*, Fig. 3). In contrast, the number of neutrophilic species that displayed an increasing niche width or a decreasing left border (H2b) was not unexpectedly high.

Shifts in the niche position with increasing latitude

16 species (38.1%) shifted their pH niche position toward more acidic sites (H3), which is not significantly more than

the nine species (21.4%) that shifted their pH niche position toward more base-rich sites ($p = 0.115$). 21.4% of the species showed unimodal niche position shifts across regions (Fig. 2, Table 3), meaning that the niche position was highest or lowest, respectively, in either one of the central regions (Germany or Denmark/Scania).

Discussion

Niche shifts in temperate forest plants are the rule

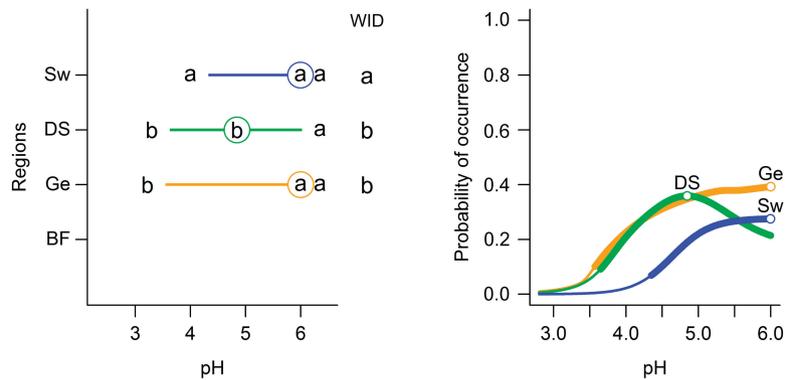
Our study provides clear evidence that most temperate forest plant species shift their realized pH niche across the nemoral zone in Europe, regarding both niche position and niche width. Comparing niches between more than two regions

Table 4. Tests of association between decreasing or increasing niche measures and the species being acidophilic or neutrophilic. In parentheses, the observed counts and expected counts are given. Each 2×2 contingency table ($n_{tot} = 42$) is tested by Boschloo's unconditional exact test. Significant p-values are printed in bold face. Each test corresponds to a specific hypothesis (Hyp.) as written in the main text. Abbreviations of niche measures: WID = niche width, LB = left border, RB = right border.

		Hyp.	Acidophilic			p	Neutrophilic			p
			Yes	No.			Hyp.	Yes	No.	
WID decreasing	Yes	1a	3 (4)	11 (10)	0.775	1b	5 (4.7)	9 (9.3)	0.420	
	No		9 (8)	19 (20)			9 (9.3)	19 (18.7)		
WID increasing	Yes	2a	6 (3.4)	6 (8.6)	0.034	2b	2 (4)	10 (8)	0.940	
	No		6 (8.6)	24 (21.4)			12 (10)	18 (20)		
LB decreasing	Yes					2b	2 (1.3)	2 (2.7)	0.301	
	No						12 (12.7)	26 (25.3)		
LB increasing	Yes					1b	7 (4)	5 (8)	0.019	
	No						7 (10)	23 (20)		
RB decreasing	Yes	1a	2 (1.7)	4 (4.3)	0.440					
	No		10 (10.3)	26 (25.7)						
RB increasing	Yes	2a	6 (3.1)	5 (7.9)	0.019					
	No		6 (8.9)	25 (22.1)						



Stachys sylvatica, n = 204, freq = 15.7%



Deschampsia flexuosa, n = 204, freq = 24%

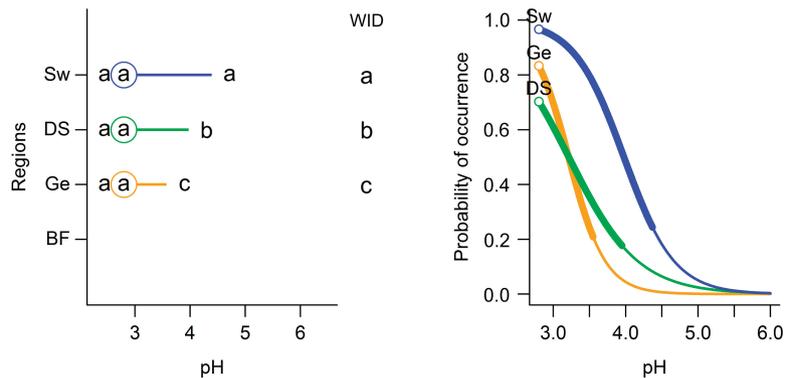


Figure 3. Response curves across regions for two example species (see Supplementary material Appendix 3 for all species), *Stachys sylvatica*, a neutrophilic species with decreasing niche width toward the north by retreating from acidic sites, and *Deschampsia flexuosa*, an acidophilic species with extending niche width toward the north by expanding toward more base-rich sites. The figure on the right gives the response curves of species per region (see Fig. 1 for abbreviations of the study regions) with niche position (open circle) and niche width (bold line). The figure on the left gives the comparison of niche measures: (WID = niche width, open circle = niche position, line = niche width with left and right borders) between regions and the significance of differences, n = number of plots included in the model, freq = frequency of species in dataset. Images from Wikimedia Commons <<http://commons.wikimedia.org>>; *Stachys sylvatica* (photo: Franz Xaver). *Deschampsia flexuosa* (photo: James Lindsey).

and using pH measurements and response curve modeling, we can confirm those studies reporting geographical niche shifts (Diekmann and Lawesson 1999, Hájková et al. 2008) in contrast with studies reporting relative niche stability (Prinzing et al. 2002, Coudun and Gégout 2005). The few invariant niche measures observed in several species cannot be taken as an indication that these species are unaffected by the suggested niche shift mechanisms, such as environmental constraints at the range margin or competitive release. Since these mechanisms are not mutually exclusive, invariant niches may result from both mechanisms acting simultaneously with a neutralizing effect. Considering this, it is even more striking that most species exhibited significant shifts in several niche measures across the regions, suggesting that either one of these mechanisms is of overriding importance for a particular species.

Although niche shifts along the pH gradient proved to be the rule, they lacked a consistent pattern across all species. Only by differentiating between acidophilic and neutrophilic species did we find consistent patterns in niche shifts. We are aware that our approach to classify species as either acido- or neutrophilic across all regions was rather pragmatic, but most species commonly considered to be indicators for either acidic or neutral conditions were correctly classified by this approach (as judged by the Ellenberg indicator values for central Europe, Table 3).

Neutrophilic species retreat from acidic sites

A majority of the neutrophilic species retreated from acidic sites with increasing latitude. Due to our short pH gradient, we cannot rule out that the neutrophilic species extended their niches toward base-rich sites beyond pH 6. We can, however, be certain that they restricted their niches in the more acidic part, which supports the hypothesis that neutrophilic species retreat toward more favorable sites when approaching their range margin. Diekmann and Lawesson (1999) also found that 2 of the 4 basophilic species reaching their range margin in southern Sweden displayed pH niche restriction toward the north. Our assumption of neutrophilic species reaching their northern range margin along our latitudinal gradient is justified for most but not all species. *Filipendula ulmaria* and *Urtica dioica* have their distribution center in northern Europe (Table 3), thus another explanation must apply for these species.

Many of the species classified as neutrophilic are known to be limited more by nitrogen availability than by soil acidity (Ellenberg 1988, Table 3). Nitrogen deposition and the effect of eutrophication on vegetation is a widely documented phenomenon across Europe (Bobbink et al. 2010) that disrupts the natural relationship between nutrient availability and soil acidity (Diekmann and Falkengren-Grerup 2002). Because nitrogen deposition is more pronounced in the southern regions of our latitudinal gradient, the niche extensions of the neutrophilic species toward the south could be explained by the increased nitrogen availability of naturally acidic and nutrient-poor sites in the south. This effect could even be strengthened by mean survey time differences in our data set, because data from Sweden and Denmark/Scania are generally older (1989 and

1984, respectively) than those of Germany and Belgium/France (1998 and 2005, respectively) and thus less affected by the amount of accumulated nitrogen (Table 2). For nitrophilic species, such as *Aegopodium podagraria*, *Stachys sylvatica* or *Urtica dioica* (Table 3), these explanations seem reasonable.

A third explanation for the niche restrictions of neutrophilic species in the north may lie in the historical legacies of the last glacial maximum. Most European plant species survived in southern glacial refuges (Bennett et al. 1991), where the relative proportion of base-rich soils was higher than in northern Europe (Reuter et al. 2008). Lenoir et al. (2010) proposed that as a result, the postglacial re-colonization of northern habitats would have been less constrained by dispersal limitation for acidophilic species than for neutrophilic species because acidic habitats would be more common and better connected. The niche restriction we observe in neutrophilic species could then be a result of a delay in filling out their potential range and ecological niche. Wasof et al. (2015) have likewise proposed this re-colonization delay as an explanation for slightly reduced climatic niches overall from the Alps towards Fennoscandia, while they interpreted especially low niche variation for acidophilic species as an indication for lower dispersal limitations than for other species.

Acidophilic species expand their niche toward base-rich sites

As latitude increased, a majority of the acidophilic species expanded their niches toward base-rich sites. According to our second hypothesis, this pattern suggests that acidophilic species are released from competition by neutrophilic species toward the north. Similarly, Coudun and Gégout (2005) observed that acidophilic species extended their niches toward more base-rich sites in northwestern France, where the regional species pool (particularly that of neutrophilic species) was lower than in northeastern France. Unfortunately, we cannot calculate the species pool for our regions from our data because the number and size of plots differ between datasets. Therefore, we cannot be sure whether competition from neutrophilic species is actually reduced in the north. However, because regional species pools of forest plants are generally assumed to decrease toward the north (Diekmann and Lawesson 1999, Wasof et al. 2013) and because we observed that neutrophilic species retreated from more acidic sites, competitive release is a likely explanation. If neutrophilic species indeed lag behind in recolonizing northern habitats, this would increase the effect of competitive release on acidophilic species. On the other hand, assuming that neutrophilic species extend their niche toward the south due to nitrogen deposition, competitive exclusion on eutrophied sites could explain the niche restrictions of acidophilic species toward the south.

In contrast to the niche shift patterns of the neutrophilic species, the patterns of the acidophilic species do not seem to support the range-margin hypothesis. A reason may be that the most favorable sites for these species are not the most acidic ones because they are actually just acid tolerant rather than truly 'acidophilic' and prefer more base-rich sites.

Although this is probably true for many 'acidophilic' species, such as *Holcus mollis* or *Poa nemoralis* (Falkengren-Grerup and Tyler 1993), the physiological pH optimum of others, such as *Deschampsia flexuosa* or *Vaccinium myrtillus*, is known to be located in the most acid part of our pH gradient (Sebald 1956).

Probably more important is the fact that our general assumption of forest plants approaching their northern range margin in boreo-nemoral Sweden is not met for many acidophilic species. Of the 11 acidophilic species, 8 actually have a Nordic distribution, meaning that they have their core distribution area rather than their range margin in the northern regions (Table 3). Therefore, optimal climatic conditions at the range core provide an alternative explanation for the fact that five of these species have their broadest niche in the northern regions, even though none of them reaches their southern range margin within our latitudinal gradient (Hultén and Fries 1986).

Niche position and local adaptation

The observed shifts in the pH niche position provide no support for the local adaptation hypothesis. Shifts in the niche position toward more acidic sites with increasing latitude were not more common than shifts to more base-rich sites. Neither did these shifts parallel or relate to the other two hypothesized patterns of niche shifts. For example, niche extensions of the acidophilic species toward more base-rich sites were not especially often accompanied by an increase in the niche position. In contrast to our results, Wasof et al. (2013) found that niche position shifts of the majority of species were directed toward more acidic sites, demonstrating local adaptation. Their approach is based on co-occurrence-based metrics to measure shifts in the pH niche and thus better reflects shifts in the multidimensional niche. Using direct measurements of the pH niche, we cannot discern a common pattern in niche position shifts. Neither did we find many shifts of the left or right border towards acidic sites in either species group, which, theoretically, could have also been regarded as an effect of local adaptation. This highlights the complexity of niche shifts, despite the explanations we found for changes in the niche width of acido- and neutrophilic species.

Conclusions

Differentiating between acidophilic and neutrophilic species is essential to find consistent patterns and plausible explanations for niche shifts along the pH gradient. Although this study does not fully reveal the mechanisms behind the observed niche shifts, we conclude that niche shifts in acidophilic and neutrophilic species result from different but interrelated mechanisms. Niche shifts of neutrophilic species could be driven by the deterioration of living conditions at their range margin in the north, by the eutrophication of acidic sites in the south or by a time-lag in the recolonization of northern habitats. The niche shifts of acidophilic species most likely are a result of competitive release (to the north) from or competitive exclusion (to the south) by neutrophilic

species. Alternatively, many acidophilic species may benefit from optimal climatic conditions in their core distribution area in the north. However, a substantial number of species displayed niche shifts that did not correspond to the main patterns, which demonstrates the complexity of niche shifts and their underlying mechanisms. More research on the proposed mechanisms behind ecological niche shifts is obviously needed. Moreover, experimental approaches are needed to unravel differences in the fundamental niches between multiple regions and the impact of these differences on the realized niche shifts.

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Supplementary material (Appendix ECOG-02051 at <www.ecography.org/appendix/ecog-02051>). Appendix 1–3.